Agriculture, Ecosystems and Environment, 16 (1986) 113—128
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

SOYBEAN GROWTH AND YIELD RESPONSE TO ELEVATED CARBON DIOXIDE

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(Accepted for publication 27 January 1986)

ABSTRACT

Rogers, H.H., Cure, J.D. and Smith, J.M., 1986. Soybean growth and yield response to elevated carbon dioxide. *Agric. Ecosystems Environ.*, 16: 113—128.

Soybeans (*Glycine max* L. Merr. 'Bragg') were grown in seeded rows in open-top field chambers and exposed continuously to a range of elevated CO_2 concentrations throughout the 1982 and 1983 growing seasons. During 1983, a water stress treatment was also imposed.

Comparison of vegetative growth with a similarly conducted pot experiment showed an increased ratio of leaf area to total top dry weight in the seeded row plants, but generally similar qualitative effects of elevated CO_2. Careful recording of mainstem leaf emergence rates and reproduction stages showed no consistent effect of CO_2 under well watered conditions, but in 1983 there was a distinct modification by high CO_2 of the water stress-induced hastening of the time to physiological maturity.

In 1982, and for the well watered plants in 1983, standing biomass at maturity was increased significantly by elevated CO_2, but harvest index decreased and yield was (statistically) unaffected by the treatment. The yield responses calculated for a doubling of the current CO_2 concentration for these well watered treatments were 1.07 and 0.93, respectively. In the water stress treatment in 1983, however, harvest index did not decrease in the presence of elevated CO_2, and a highly significant yield response occurred (1.41 at 700 $\mu l\ l^{-1}$).

INTRODUCTION

Recent global carbon cycle models project a range of possible atmospheric carbon dioxide (CO_2) concentrations in year 2075 of approximately 500—1500 $\mu l\ l^{-1}$, with a median of about 700 $\mu l\ l^{-1}$ (Edwards et al., 1984). In order to evaluate the impact of this change on agricultural productivity,

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0167-8809/86/$03.50

work has recently focused on the direct effects of elevated CO_2 on long term growth and yield of crop plants (Lemon, 1983). Until very recently, however, field studies have been lacking due to a technical inability to generate the large scale test atmospheres required. In recent years this has been overcome at several research sites (Kimball, 1983; Rogers et al., 1983b; Havelka et al., 1984) and equipment for the study of crop response to CO_2 enrichment in the field is now available.

Soybeans were exposed to a range of above-ambient concentrations of CO_2 in open-top field chambers throughout the 1982 and 1983 growing seasons, and in 1983, a water stress treatment was also included. In this paper, vegetative growth observations are compared with those from a previous CO_2 enrichment study for soybeans conducted in pots in open-top chambers, and the yield data from the field are presented against a background of yield results obtained under a wide variety of environmental conditions.

MATERIALS AND METHODS

Soybean plants (*Glycine max* L. Merr. 'Bragg') were grown in open-top field chambers (Rogers et al., 1983b). Each chamber consisted of a cylindrical aluminum frame (3 m in diameter × 2.4 m in height) covered with PVC film Roll-A-Glass with a 45° frustum attached at the top. Air with the desired CO_2 concentration was supplied day and night through perforations in the inner wall of the lower half of the chamber. Air was adjusted to the proper CO_2 level with pure CO_2 fed from a supply tank of pure liquid CO_2. Mixing occurred in a fan-driven plenum box where the air and CO_2 were brought together and blown into the chamber (Rogers et al., 1983b). Gas samples were drawn from each plot at 10 cm above canopy level 3 times hourly and adjustments in CO_2 dispensed to each chamber were made twice daily based on the most recent 3-h means. A full account of CO_2 measurement and control has been given (Rogers et al., 1983b).

1982 Experiment

In 1982, there were two replicate plots per CO_2 treatment, randomly arranged in each of two blocks. Seasonal daytime 0500—1900 h EST) mean CO_2 concentrations for the 6 CO_2 treatments were 348 $\mu l\ l^{-1}$ (open plot without chamber), 349 $\mu l\ l^{-1}$ (ambient chamber), 421 $\mu l\ l^{-1}$, 486 $\mu l\ l^{-1}$, 645 $\mu l\ l^{-1}$ and 946 $\mu l\ l^{-1}$. Extremely wet weather delayed planting until 29 June. Six days after planting (DAP), the chambers were set in place and at 8 DAP, CO_2 dispensing and monitoring began. Water was applied to the plots whenever tensiometers (one at 30 and one at 45 cm) showed soil moisture tensions greater than 50—60 centibars. From 1 of the 2 replicate plots within each block, sequential harvests were made for growth analysis. These harvests were of at least 8 plants each (the first 2 were thinning harvests) and occurred on Days 14 (seedling), 29 (mid-vegetative), 76 (early pod fill), 125 (physiological maturity) and 140 (harvest maturity, when all pods were brown). The other replicate plot within each block was reserved for yield harvests only (the last 2 dates). The yield harvests at 125 and 140 DAP consisted of at least 0.75 m of row 0.3 m inside the chamber wall from each of the 2 replicates within each block. Seeds were removed from pods harvested at 140 DAP for calculation of harvest index (seed dry wt/total top dry wt).

1983 Experiment

In 1983 there were two blocks, with one replicate of each of two watering regimes randomly arranged in each block. The seasonal daytime 0500—1900 h EST) means for the 5 CO_2 treatments were 349 $\mu l\ l^{-1}$ (open plot without chamber), 346 $\mu l\ l^{-1}$, 424 $\mu l\ l^{-1}$, 505 $\mu l\ l^{-1}$ and 650 $\mu l\ l^{-1}$. Planting occurred 6 June, and chambers were in place and CO_2 dispensing and monitoring began by 10 DAP. Semi-open platforms were placed between the rows to minimize compaction of soil between the rows. Rain covers were placed over the tops of the stressed plots during rain, or overnight if rain threatened, in such a way that the air flow through the chambers was not affected. Non-stress plots were irrigated whenever tensiometers (2 at 30 cm and 2 at 45 cm depth in each plot) reached 20—30 centibars. For the first 50 days, only a mild water stress was permitted to develop in the stress plots, irrigation taking place when the tensiometers showed soil moisture tensions of 70—80 centibars. After 50 DAP irrigation took place only on days when plants were seen to be wilted in the early mornings.

In both years, plants were sprayed weekly with appropriate insecticides and weeds were controlled by hand within the test plots. Plants were tied up to avoid lodging. Stem and leaf samples were oven-dried for at least 72 h at 55 ± 5°C and pods were dried at about 21°C. Leaf areas were measured photometrically with automatic area meters. In both years, plants were thinned to a density of 15 m^{-1}, and rows were 96.6 cm apart. However, in 1982, the chambers were placed over the rows such that two main rows of maximum length were centered in the chamber; growth of the two "border rows" was necessarily disrupted by chamber walls and consequently their usefulness as border rows was compromised. In 1983, the chambers were placed so that there was one main row down the center of the chamber with two good border rows. Samples were collected only from the center row.

Growth Analysis

The following growth functions were calculated from above-ground mass data according to Kvet et al. (1971):

NAR (mean net assimilation rate) = dry matter accumulation rate per unit leaf area

LAR (mean leaf area ratio) = ratio of leaf area to total top dry matter
RGR (mean relative growth rate) = dry matter accumulation rate per unit dry matter

NAR, LAR and RGR from a 1981 pot experiment (see Rogers et al., 1984a) were recalculated deleting root dry weights for comparison with values obtained from the 1982 field plots. (For detailed data from 1982 field study see Rogers and Bingham, 1982). In the pot study, the intervals were (1) 5—14 days, (2) 14—49 days and (3) 49—84 days. In the field study the intervals were (1) 5—14 days, (2) 14—29 days and (3) 29—76 days. Thus, although in both studies the same genotype and the same exposure system were used, they were performed in different years. Also, the growth characteristics of seeded row plants in the second and third intervals reflect the behavior of younger plants than those in the pots, as well as the behavior of plants grown without apparent restriction of root growth.

Statistics and Response Ratio Calculations

Regression analyses were performed by the least squares method (Neter and Wasserman, 1974). In Tables, I, II and III a significant water stress

TABLE I

1982 harvest data for 'Bragg' soybeans grown in open top chambers at 5 CO_2 concentrations. $N = 8$

CO_2 ($\mu l\ l^{-1}$)[1]	Stem dry wt. ($g\ m^{-1}$)	Pod dry wt. ($g\ m^{-1}$)	Pod number (m^{-1})	Harvest index[2]
348	263	438	1032	0.47
349	395	744	1509	0.49
421	456	803	1698	0.49
496	482	739	1658	0.45
645	526	835	1854	0.46
946	636	873	2173	0.42
$s_{\bar{x}}$	25	57	107	0.01
CV (%)	13	14	15	4.3
b_0	132±31	438±57	666±126	0.51±0.01
$b_{chamber}$	152±30[3]	360±63[3]	512±121[3]	0.01±0.01
b_{linear}[4]	377±52	NS	1049±214	−0.01±0.02
$b_{quadratic}$	NS	NS	NS	NS
R^2	0.99	0.94	0.99	0.88

[1]The first CO_2 value (348) is from the open plots (no chambers); other values are from within chambers. Values for CO_2 are seasonal daytime means.
[2]Harvest index is from sampling at harvest maturity only. Other variables represent average values from harvests at physiological maturity and harvest maturity.
[3]Significant F (0.95 level) for chamber effects.
[4]Linear coefficients and their standard errors should be multiplied by 10^{-3}.

TABLE II

1983 harvest data for stressed (S) and non-stressed (NS) "Bragg" soybeans grown in open plots and in open-top chambers at 4 CO_2 concentrations $N = 2$

CO_2 ($\mu l\ l^{-1}$)[1]	Stem dry wt. ($g\ m^{-1}$)		Pod dry wt. ($g\ m^{-1}$)		Pod number (m^{-1})		Harvest index	
	S	NS	S	NS	S	NS	S	NS
349	317	425	335	405	759	1004	0.36	0.35
346	339	488	464	683	991	1506	0.40	0.42
424	432	613	584	699	1049	1509	0.40	0.38
505	426	603	602	661	1120	1459	0.41	0.38
650	522	682	661	654	1325	1510	0.40	0.35
$s_{\bar{x}}$	32.8		28.5		60.7		0.01	
CV (%)	9.6		7.0		7.0		3.9	
b_o	101±52	225±52	131±52	405±28	516±81	864±81	0.40±0.01	0.38±0.1
$b_{chamber}$	69±35[2]		165±36[2]	269±32[2]	354± 54[2]		0.05±0.01[2]	
b_{linear}[3]	553±123		585±127	NS	550±190		−0.11±0.03	
$b_{quadratic}$	NS		NS	NS	NS		NS	
R^2	0.96		0.98	0.99	0.97		0.90	

[1]The first CO_2 value (349) is from the open plots (no chambers); other values are from within chambers. Values for CO_2 are seasonal daytime means.
[2]Significant F (0.95 level) for chamber effect.
[3]Linear coefficients and their standard errors should be multiplied by 10^{-3}.

TABLE III

Protein, oil and fiber content of 'Bragg' soybean seeds produced in open top chambers at various CO_2 concentrations in 1982 (N=8) and 1983 (N=2). In 1983 S = water stressed and NS = non-stressed treatments[1]

1982				1983						
CO_2 ($\mu l\ l^{-1}$)	Protein (%)	Oil (%)	Fiber (%)	CO_2 ($\mu l\ l^{-1}$)	Protein (%)		Oil (%)		Fiber (%)	
					S	NS	S	NS	S	NS
348	40.6	17.6	41.8	349	44.8	43.4	18.0	18.9	37.1	38.0
349	40.8	17.5	41.7	346	41.6	43.0	19.4	19.0	39.1	38.0
421	40.0	17.6	41.4	424	42.8	43.1	19.0	18.9	38.3	38.0
496	41.2	17.2	41.6	505	41.5	43.0	19.7	18.6	39.0	38.4
645	41.1	17.3	41.6	650	41.1	42.5	19.4	19.1	40.0	38.4
946	41.2	17.0	41.9							
$s_{\bar{x}}$	0.25	0.24	0.12		0.39		0.37		0.39	
CV (%)	1.2	3.4	0.9		1.29		2.72		1.44	
b_o	40.8	17.4	41.7		43.0	44.8±0.4	19.0		38.7	37.1±0.4
$b_{chamber}$	NS	NS	NS		NS	−3.1±0.4	NS		NS	1.8±0.4[3]
b_{linear}	NS	NS	NS		NS	NS	NS		NS	NS
$b_{quadratic}$	NS	NS	NS		NS	NS	NS		NS	NS
R^2	NS	NS	NS		NS	0.86	NS		NS	0.99

[1] Analysis performed by Dr. Jim Cavins, Research Chemist, Horticultural and Special Crops Laboratory, Peoria, IL 61604.
[2] The first CO_2 value is from the open plots (no chambers); other values are from within chambers. Values for CO_2 are seasonal daytime means.
[3] Significant F (0.95 level) for chamber effect.

TABLE IV

Yield Response Ratios (1000 $\mu l\ l^{-1}$/350 $\mu l\ l^{-1}$) and changes in harvest index for soybeans tested at CO_2 concentrations > 1000 $\mu l\ l^{-1}$ under different experimental conditions

Experiment	Genotype[1]	Growth condition	CO_2 treatments ($\mu l\ l^{-1}$)[2]	Response ratio 1000/350	Change in HI
1a Maddox, 1974	Bragg (VII, d)	pot with vermiculite and perlite; small chambers within a greenhouse, enriched after 12 days post-flowering	360, 1300	1.13	0.59→0.58
1b Maddox, 1974	Forrest (V, d)	same conditions as above	360, 1300	1.02	0.58→0.59
1c Maddox, 1974	D69—B5 (VI, d)	same conditions as above	360, 1300	1.05	0.60→0.61
1d Maddox, 1974	Lee 68 (VI, d)	same conditions as above	360, 1300	0.97	0.59→0.60
2a Cooper and Brun, 1967	Hark (I, i)	3 plants per pot with soil; supplemented winter greenhouse light	350, 1350	1.37	0.61→0.57
2b Cooper and Brun, 1967	Chippewa 64 (I, d)	same conditions as above	350, 1350	1.26	0.59→0.55
3 Hardman and Brun, 1971	Hark (I, i)	spaced plants in ground in open-top chambers	350, 1200	1.28	0.32→0.27
4 Ackerson et al., 1984	Wye (IV, i)	seeded rows, open-top chambers	"AMB" (= 350), 1200	1.20	0.42→0.43
5 Havelka and Hardy, 1976	Kent & Clark (IV, d)	seeded rows, open-top chambers (enriched Days 35—105)	"AMB" (= 350), "800—1200" (= 1000)	1.78 (pods)	0.47→0.56 (pods)
6a Havelka et al., 1984	Kent (IV, d)	seeded rows, open-top chambers (enriched Days 22—maturity)	330, 1200	1.60	0.32→0.34
6b Havelka et al., 1984	Ware (IV, d)	same conditions as above	330, 1200	1.41	0.34→0.39

[1]The Roman numeral refers to maturity grouping and 'd' or 'i' refers to determinate or indeterminate growth habit, respectively.
[2]From 350 to 1000 ppm CO_2.

TABLE V

Yield Response Ratios (700 $\mu l\ l^{-1}$/350 $\mu l\ l^{-1}$) and changes in harvest index for soybeans tested at CO_2 concentrations < 1000 $\mu l\ l^{-1}$ under different experimental conditions

Experiment	Genotype	Growth condition	CO_2 treatments ($\mu l\ l^{-1}$)	Response ratio 700/350	Change in HI
1a Sionit, 1983	Ransom (VII, d)[1]	pot with gravel and turface; controlled environment; light 550 $\mu E\ m^{-2}\ s^{-1}$; 1/2 Hoagland's	350, 675	2.34	0.73→0.69
1b Sionit, 1983	Ransom (VII, d)	same conditions as above except 1/8 Hoagland's	350, 675	2.09	0.73→0.73
2 Jones et al., 1984	Bragg (VII, d)	SPAR units, seeded rows	330, 450, 600, 800	1.35	0.31→0.30
3 Acock et al., 1982	Forrest (V, d)	SPAR units, seeded rows	330, 450, 600, 800	1.38	0.44→0.45
4 Acock et al., 1983	Bragg (VII, d)	SPAR units, seeded rows	330, 450, 600, 800	0.14 (pods)	0.79→0.73 (pods)
5 Rogers et al., 1983a	Ransom (VII, d)	pots with soil in open-top chambers	340, 520, 718, 910	1.31	0.58→0.55
6 Rogers et al., 1981	Bragg (VII, d)	pots with soil in open-top chambers	332, 428, 534, 623, 772, 910	1.16	0.51→0.47

7a Rogers and Bingham, 1982	Bragg (VII, d)	pots with soil in open-top chambers; well watered	349, 421, 496, 645, 946	1.03	0.50→0.43
7b Rogers and Bingham, 1982	Bragg (VII, d)	same condition as above except water stressed	349, 421, 496, 645, 946	1.14	0.54→0.47
8a Israel and Rogers, 1982	Bragg (VII, d)	pots with perlite; open-top chambers; *Rhizobium* strain USDA 110	349, 421, 496, 645, 946	1.08	— —
8b Israel and Rogers, 1982	Bragg (VII, d)	same conditions as above except *Rhizobium* strain USDA 31	349, 421, 496, 645, 946	0.95	— —
9 Rogers, Cure and Smith (this report)	Bragg (VII, d)	seeded rows, open-top chambers (1982)	349, 421, 496, 645, 946	1.07	0.49→0.45
10a Rogers, Cure and Smith (this report)	Bragg (VII, d)	seeded rows, open-top chambers (1983); well watered	346, 424, 505, 650	0.93	0.41→0.34
10b Rogers, Cure and Smith (this report)	Bragg (VII, d)	same as above except water stressed	346, 424, 505, 650	1.43	0.40→0.40

[1]The Roman numeral refers to maturity grouping, and 'd' or 'i' refers to determinate or indeterminate growth habit, respectively. From 350 to 700 ppm CO_2.

effect was indicated for a variable by the presence of separate Y-intercepts (b_o) for the stressed (S) and non-stressed (NS) treatments, and a CO_2 $\times$ stress interaction was also described by separate parameter estimates for S and NS plants.

In Tables IV and V, seed yield data from the listed references were regressed against CO_2 concentration, and yield response ratios were calculated from predicted yield values for 1000 and 700 $\mu l\ l^{-1}$ CO_2, respectively, relative to yield at 350 $\mu l\ l^{-1}$ CO_2. Linear regressions were employed where only two data points were provided (Table IV). Either linear or quadratic models were used, where statistically appropriate, in cases where more data points permitted (Table V). Since yield response to CO_2 concentration departs from linearity in the range 350—1300 $\mu l\ l^{-1}$, the response ratios at 1000 $\mu l\ l^{-1}$ (based on data obtained at 350 and 1300 $\mu l\ l^{-1}$) are probably underestimates. Nevertheless, the ratios in Table V are internally comparable.

RESULTS AND DISCUSSION

Row Crop Studies: 1982—1983

In 1982, stem dry weight and pod number increased in a linear fashion with increasing CO_2 concentration as denoted by significant, positive linear regression coefficients in Table I. Harvest index (HI) decreased, however, and although there was a definite trend towards increasing pod dry weight, no statistically significant effect of CO_2 enrichment on yield was observed. A similar pattern of responses occurred for the non-stressed plants in 1983, i.e. an increase in stem dry weight with increasing CO_2 concentration, together with a decreasing harvest index and a lack of yield response to CO_2 (Table II). However, the stressed plots in 1983 showed clear effects of the chronic water stress on stem dry weight and pod number, as denoted by the presence of different intercepts (b_o), but no stress $\times$ CO_2 interaction. For pod yield, however, our analysis indicated both a water stress effect and a significant CO_2 $\times$ water stress interaction, resulting in separate equations for the two treatments. At 350 $\mu l\ l^{-1}$, the pod dry weight decrease due to water stress was about 175 g m^{-1}, but this effect became insignificant at higher CO_2 concentrations.

Seed protein and oil content were lower in 1982 than in 1983, and there was a significant effect of water stress on protein content in 1983, but there was no effect of elevated CO_2 on seed composition in either year (Table III). Moreover, further analysis of the oil fraction of the 1982 seed showed no effect of elevated CO_2 on fatty acid composition (R. Wilson, unpublished data, 1983).

Using predicted values obtained from the parameter estimates in Tables I and II, total standing biomass produced in ambient-level CO_2 chambers was quite similar between the 1982 crop and the non-stressed 1983 crop (1189 g m^{-1} in NS 1983 plots vs. 1139 in 1982). However, HI was much greater in 1982 and yield was therefore greater. The reason for this difference in HI is uncertain, but it may be related to the different row configurations within the chambers described in "Methods".

Figure 1 illustrates the relative effects of continuous exposure to elevated CO_2 on the yield of soybeans grown under conditions as close as possible to field conditions. Water stress was not imposed in 1982. Only in stressed plots in 1983 was CO_2 effective in increasing pod yield, suggesting that increased yield brought about by elevated CO_2 is largely due to changes in plant water relations.

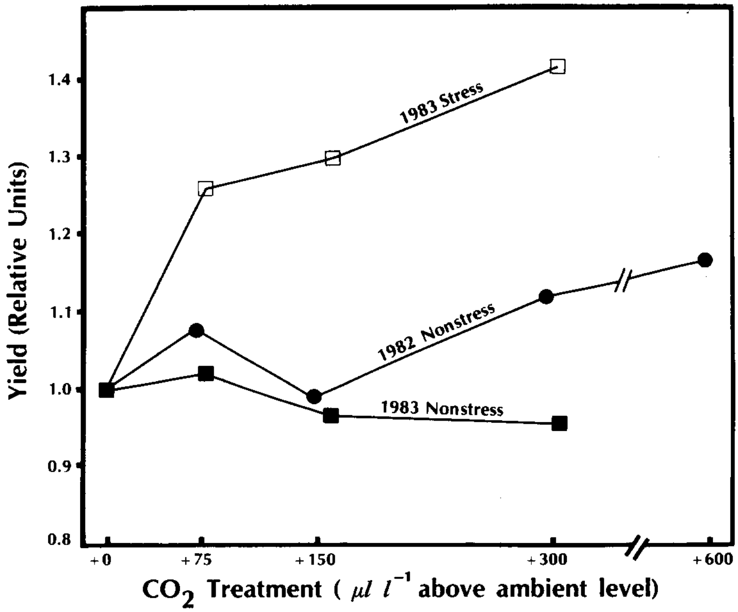

Fig. 1. Relative pod yield for 'Bragg' soybeans grown in the field in open-top chambers at elevated CO_2. The 1982 experiment did not include water stress treatments.

Elevated CO_2 had a small accelerating effect on the rate of leaf initiation in both years, resulting in the addition of one vegetative mainstem node before meristems were converted to the reproductive mode (21 vs. 20 nodes in 1982; 23 vs. 22 nodes for non-stressed plants in 1983). There was also a trend toward slightly faster expansion of the leaves in high CO_2 in both years. Although the same number of mainstem leaves was eventually present in the stressed vs. non-stressed plants in 1983, the stress treatment slowed production of the last leaves by almost a week at low CO_2 and by 3 days at 650 ppm. All reproductive stages in high CO_2 occurred slightly behind those for control plants in 1982. In 1983, however, physiological maturity was accelerated by 4 days by high CO_2. Water stress also accelerated maturity, by 7 days at the low CO_2 concentration, but this effect of water stress on time to maturity was not observed at high CO_2. Yellowing of leaves was observed to occur more rapidly at high CO_2 concentrations both years.

Comparison with Pot Experiments

Since so much CO_2 work has been done with potted plants, it was of interest to compare some vegetative growth characteristics of 'Bragg' soybeans obtained in the 1982 field study with those obtained with the same genotype similarly exposed to CO_2-enriched air in open-top field chambers, but grown in pots. The objective was to compare the effect of elevated CO_2 on RGR (mean relative growth rate), NAR (mean net assimilation rate) and LAR (mean leaf area ratio) of plants grown in 10-inch pots (see Rogers et al., 1984a) with plants grown with no apparent root restriction. These vegetative growth functions were calculated according to Kvet et al. (1971) over three intervals (see "Methods").

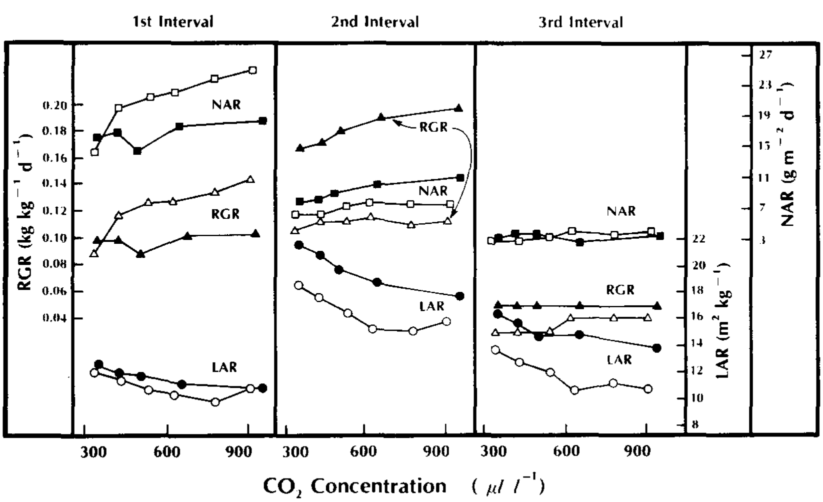

Fig. 2. RGR (△,▲), LAR (○,●) and NAR (□,■) for 'Bragg' soybeans grown in pots in 1981 (open symbols) and in the field in 1982 (closed symbols) in open-top field chambers at elevated CO_2 concentrations.

The first growth interval (Fig. 2) showed a small apparent decrease in LAR at higher CO_2 concentrations in both the 1982 seeded row crop study and the 1981 potted plant experiment. Bearing in mind that chamber placement and CO_2 dispensing in the 1982 field study did not begin until 8 days after planting, it is perhaps not surprising that in the first interval there was only a trend for increasing NAR and therefore (since RGR = LAR × NAR) for increasing RGR with increasing CO_2 concentration. In contrast, in the 1981 pot study, where treatments were imposed at seed planting, there was a very marked effect of CO_2 concentration on NAR and therefore on RGR in the same time period.

In the 2nd interval, the RGR of the potted plants, which remained constant across CO_2 treatments, reflected about equally the influence of the increasing NAR and decreasing LAR. In this interval, LAR was substantially higher in the seeded row crop than in the pot study, although it responded to CO_2 treatments similarly to the potted plants. NAR, however, was not only higher in the row crop than in the pot study, the response to CO_2 continued at the highest treatment level, whereas in the pot study the NAR no longer responded to CO_2 concentration above 623 $\mu l\ l^{-1}$. The RGR of the row crop was, therefore, not only much higher than in the pot study (0.17 vs. 0.11 at ambient CO_2), but due to the contribution of NAR, it increased with increasing CO_2 concentration as well, reaching 0.20 at 945 $\mu l\ l^{-1}$.

In the third interval, the influence of CO_2 on NAR and RGR was no longer observed in either study, although it was still apparent in the LAR in both studies. The influence of elevated CO_2 was qualitatively similar in both growth conditions: lowered LAR and stimulated NAR and RGR early in the season with decreasing effect as vegetative growth proceeded. The major differences in growth observed in the field-grown soybeans, for which root growth was presumably unrestricted, were (a) highly increased LAR and (b) higher NAR values at high CO_2 concentrations in the 2nd interval. In comparing growth of 'Bragg' soybeans under these two systems, it is interesting that Sionit et al. (1984) found for soybeans during pod filling an essentially linear leaf photosynthetic response to light up to 1600 $\mu E\ m^{-2}\ s^{-1}$ for field grown soybeans, whereas photosynthesis for potted plants in neighboring chambers leveled off at 800 $\mu E\ m^{-2}\ s^{-1}$. The relative effect of high CO_2 was much greater for the potted plants.

Yield Response

The 1982—83 field experiments were conducted to directly address the issue of elevated carbon dioxide effects on field crop growth, behavior and yield. Field conditions were therefore maintained as closely as possible. However, most work with CO_2 effects on soybeans has been done in pots, whether in open-top chambers or greenhouses in controlled environment chambers, or in outdoor controlled environment chambers (SPAR units). A survey of all CO_2 soybean yield work for which growth conditions were available was made. This work fell naturally into two classes: experiments in which one very high CO_2 concentration (> 1000 $\mu l\ l^{-1}$) was compared with a CO_2 concentration near ambient (Table IV), and those in which several CO_2 levels were maintained, all between ambient and 1000 $\mu l\ l^{-1}$ (Table V). Only in the work of Sionit (Table V) was there a single elevated CO_2 treatment which was also less than 1000 $\mu l\ l^{-1}$. The seed yield data from these studies were regressed against CO_2 concentration, and the yield response ratios were calculated from predicted values at 1000 $\mu l\ l^{-1}$/350 $\mu l\ l^{-1}$ using a linear model (Table IV) and at 700 $\mu l\ l^{-1}$/350 $\mu l\ l^{-1}$ using either a linear or quadratic model, as statistically appropriate (Table V).

Harvest index (HI) was either unaffected or decreased in all reports in Tables IV and V, except those in which exposure was limited to later stages of growth (Table IV, Experiments 4—6). These latter increases in HI due to CO_2 treatment during reproductive growth were also observed by Hardman and Brun (1971). Soybean appears to be the only crop species for which CO_2 usually decreases HI (Cure, 1985). Increases in HI due to increased CO_2 concentration have been reported for barley (Gifford et al., 1973), corn (Goudriaan and deRuiter, 1983; Rogers et al., 1983a) rice (Cock and Yoshida, 1973; Yoshida, 1973) and wheat (Gifford, 1977, 1979; Sionit et al., 1980, 1981; Goudriaan and deRuiter, 1983).

Further careful study of Tables IV and V shows no clear, substantial effects of genotype or degree of determinacy on the response ratios. If there is such an effect, it is overshadowed by the apparent effect of growth conditions for both the 1000/350 $\mu l\ l^{-1}$ yield response ratio (Table IV, cf entries 1 a—d, 2 a—b, 4—6 b) and the 700/350 $\mu l\ l^{-1}$ yield response ratio (Table V, cf entries 1 a—b, 2—4, 5—8 b and 9—10 b). The means from each of the experiments were pooled to obtain an overall response at 700 $\mu l\ l^{-1}$ of 1.29 ± s.e.m. 0.11 and at 1000 $\mu l\ l^{-1}$ of 1.35 ± s.e.m. 0.11.

Although we have no unequivocal evidence as to the effect of such field-associated stresses as high leaf temperature on the photosynthetic or growth response to elevated CO_2, we now have evidence, accumulated mostly from controlled environment experiments, that the growth response to CO_2 is dampened under conditions of nutrient stress for soybeans (Imai and Murata, 1978; Sionit et al., 1981; Williams et al., 1981; Patterson and Flint, 1982; Goudriaan and deRuiter, 1983; Sionit, 1983). Water stress may be unique among commonly encountered field stresses because of the positive effect of elevated CO_2 on water-use efficiency for soybeans (Rogers et al., 1983a; Valle et al., 1985) as well as other species (Carlson and Bazzaz, 1980). Thus, growth response of soybeans to CO_2 should be enhanced in dry conditions as has been shown for wheat (Gifford, 1979). The data from our 1982—83 field studies (this report) suggest that the effects of elevated CO_2 on growth and yield of field-grown soybeans may be limited by the various stresses associated with field conditions except in the presence of water stress.

In order to predict with confidence how plants will respond to elevated CO_2 concentration in the field, we must first, make better use of controlled environment facilities to explore interactions of environmental factors (e.g. temperature, light, root restrictions on growth) and their impact on the CO_2 response, and second, characterize our field test facilities more fully so as to understand the differences illustrated here both from year to year and from site to site.

ACKNOWLEDGEMENT

Funding for this work was by the Department of Energy through interagency No. DEAI-01-81-ERG0001 to the USDA.

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